Field Homology: Still a Meaningless Concept

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Introduction

The cytoarchitectural organization of vertebrate brains can differ markedly across species, and this divergence is most striking in the telencephalon. In mammals, the telencephalon harbors the neocortex, a 6-layered sheet of neurons and other cell types thought to be largely responsible for mammalian cognitive abilities. The non-mammalian telencephala, in contrast, comprise a range of divergent tissue architectures that do not morphologically resemble the neocortex at all. Many neuro-anatomists, including myself [Briscoe and Ragsdale, 2018a], have sought to understand the evolutionary relationships of telencephalic structures in order to explain the evolutionary history of the neocortex and, by extension, the origins of human cognitive faculties [Striedter, 1997; Aboitiz and Montiel, 2007; Butler et al., 2011; Bruce, 2012; Jarvis et al., 2013; Suzuki and Hirata, 2013; Dugas-Ford and Ragsdale, 2015; Puelles et al., 2017]. However, and as a result of the conceptual problems inherent in comparing very different biological characters, the history of comparative telencephalon anatomy has been a veritable circus of conflicting ideas [Striedter, 1997]. In this short essay, I aim to eliminate one of them.

Field homology has emerged as a framework for describing the evolution of vertebrate brains, and it is based upon the proposed developmental origins of neuro-anatomical characters within the embryo [Nieuwenhuys and Puelles, 2016]. In this view, the developing nervous system is regionalized into a grid-like series of territories, or developmental fields, along antero-posterior and mediolateral coordinates. The fate of adult structures is specified within these fields by conserved transcription factor codes, and each developmental field then gives rise to a specific set of derivatives. As the most crucial claim, if it can be demonstrated that 2 or more vertebrates share a homologous developmental field, then the products of that field in each species are considered to be homologous “as a field” [Puelles and Medina, 2002]. The potential for homology of two compared brain regions – whether they are the same thing – is therefore determined solely by whether they arise from equivalent positions in a shared developmental Bauplan [Nieuwenhuys and Puelles, 2016].

This interpretation of homology is deeply problematic, and its continued application represents a conceptual impediment to future progress in comparative neuroscience. In particular, field homology (1) does not describe either the similarity

or common ancestry of compared characters, (2) conflates the independent hierarchical levels of homology, and (3) provides no opportunity for insights into the mechanisms of brain structural evolution. It is, in short, meaningless [Northcutt, 1999].

Similarity, Essentialism, and Evolutionary Preformationism

Homology, as conceived by most comparative biologists, refers to similarity due to common ancestry [Patterson, 1988; Hall, 1994]. Homology refers to similarity, and this component of the definition is essential for a meaningful and practical homology concept. The existence of similarities among organisms – the observation that living things resemble each other and are not instead completely different – itself provides the evidence for the common descent of life and the things it is made of. When we compare two extant species and

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seek homologies, we are searching for those shared similarities present in their last common ancestor and preserved in their respective lineages. The dissimilarities, or the species-specific properties acquired only after divergence, cannot be considered homologous because they were not present in the last common ancestor.

Field homology differs substantially from this version of homology. Field homology states that neuroanatomical characters are homologous if they arise from equivalent developmental fields, but both similarity and common ancestry are conspicuously absent from the definition. Even if a particular developmental field is conserved in two species, the adult derivatives of that field may not be, especially in the telencephalon. Field homology can therefore be used erroneously to define evolutionarily unrelated, species-specific characters as homologs by lumping similarities and dissimilarities indiscriminately together. To deal with this problem, some authors have argued that homology, or “true sameness,” does not require similarity at all [Puelles and Medina, 2002; Puelles and Ferran, 2012]. This idea is a clear expression of essentialism, a doctrine that the identity and homology of two characters depends upon some essence that transcends their actual physical properties. Consequently, field homology cannot be expected to convey any information about a character beyond the relative location of its progenitors.

Every biological character must have an origin and can be said to exist only within one particular clade: the clade descended from the first species to possess that character. To state that a character has a homology outside of that clade is to push the origin of that character inappropriately far back into evolutionary time, to a more remote common ancestor where it was not present. The field homology concept enables such an infinite evolutionary regress: if similarity is immaterial to homology, then there is no basis for judging which species possess a character of interest and no means to infer when that character arose or when it has been lost. The line that separates when a character exists, and when it does not, disappears. It has been suggested, for example, that all vertebrate embryos possess exactly the same set of developmental fields in an invariant organizational Bauplan [Albuixech-Crespo et al., 2017]. The rather alarming implication is that every part of the nervous system in ev-

ery vertebrate can be said to possess a homology in every other vertebrate, that everything was present since the beginning of the vertebrates or earlier, and that there can be nothing new in brain evolution. A homology concept that generates such extreme conclusions provides little descriptive or explanatory value to comparative neuroanatomy.

The Hierarchical Organization of Homologies: Neural Circuit Evolution and the Origin of the Neocortex

Some proponents of field homology hold that “similarity of connections is irrelevant with regard to homology” [Puelles et al., 2017]. This assertion is unequivocally false – connections are either homologous or they are not, and to state that they are irrelevant is to simply avoid the question of their origins. We can test whether neuronal connections are homologous through the same means by which we would test homology of any other compared characters at any level of organization: by assessing their degree of similarity and by determining their phylogenetic distributions [Patterson, 1988; Striedter and Northcutt, 1991; Briscoe et al., 2018]. In other words, it is possible to infer the phylogenetic origins of a connective trait through comparative analyses. More importantly, the recognition of homology versus non-homology at the level of neuronal circuitry is essential for any mechanistic explanation of brain structural evolution. That is, to understand the evolution of a neuroanatomical structure, we must understand the evolution of its components.

Birds and nonavian reptiles do not possess a neocortex, but their telencephala do contain several classes of excitatory neuronal cell types that are remarkably similar to mammalian neocortical neurons in terms of their connectivity patterns [Briscoe et al., 2018; Briscoe and Ragsdale, 2018b]. Rather than being stacked into a 6-layered cortical structure, these avian and reptilian neuronal cell types are generally organized into clustered nuclei within a structure called the dorsal ventricular ridge. Put simply, what differs across mammalian, avian, and reptilian telencephala is the spatial distribution of their neuronal cell types and circuitry. Thus, an explanation for the origins of the neocortex and of the dorsal ventricular ridge is one that accounts for the

origins of their component neuronal cell types and the developmental mechanisms that arrange them differentially. I elaborated upon a hypothesis, initially proposed by Karten [1969], that the similarities seen at the level of neuronal cell types reflect homology due to common descent: the neocortical neuronal cell types are ancestral to amniotes, and the neocortex originated in stem mammals through the developmental reorganization of these preexisting cell types [Briscoe and Ragsdale, 2018a]. The field homology concept, by ignoring homologies at all levels besides developmental fields, is fundamentally inadequate for providing such explanations for evolution at the levels of neuroanatomical structures or neuronal cell types.

Conclusions

It is possible to identify homologous neuroanatomical characters and then to ask whether they are also developmentally specified through conserved patterning mechanisms [Briscoe and Ragsdale, 2018a]. It is even possible to identify homologous developmental patterning mechanisms and to ask whether these give rise to homologous neuroanatomical characters [Pani et al., 2012]. Such questions address homologies at separate and evolutionarily independent levels of biological organization. Homology at the level of progenitor domains cannot be considered a sufficient condition for the homology of adult derivatives, as this would uncouple the homology concept from evolutionary relatedness and render it descriptively meaningless. Field homology, as defined in the references described here, must be rejected in favor of a hierarchical model of evolution.

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